



Full Length Article

Genetic Characterization of Stripe Rust and Yield Traits in Bread Wheat

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Abstract

The insight into the nature of gene action, involved in the expression of a trait of interest, is essential to a plant breeder for deploying a judicious breeding program. The objective of this study was to study the inheritance (additive vs., dominance) of stripe rust resistance and yield traits in wheat through diallel analysis. Six wheat cultivars *i.e.*, Pirsabak-85, Khyber-87, Saleem-2000, Pirsabak-04, Pirsabak-05 and Shahkar-13 were crossed in a half diallel fashion during 2014-2015, and advanced to F₂ generation during 2015-2016. Parental genotypes along with their F₁ and F₂ populations were evaluated during 2016-2017 through randomized complete block design with three replications. Genotypes differed significantly ($p \leq 0.01$) for all the traits in F₁ and F₂ generations. Additive-dominance model was partially adequate for resistance to stripe rust and yield-related traits. Greater values of additive (D) than dominance (H₁, H₂) components of genetic variance, average degree of dominance and Vr-Wr graphs revealed that stripe rust resistance and yield traits were primarily controlled by additive gene action except for grain yield in F₁ and area of flag leaf in the F₂ generation which governed by overdominance. In loci, unequal proportions of positive (H₁) and negative (H₂) alleles revealed the asymmetrical distribution of genes in parental genotypes for stripe rust resistance and yield traits. The preponderance of additive gene action suggested that selection could be made in early segregating generations for improving resistance against stripe rust to enhance wheat yield. © 2019 Friends Science Publishers

Keywords: Diallel cross; Gene action; Genetic variance; Heritability; **Stripe rust**; Yield traits

Introduction

Wheat (*Triticum aestivum* L.) is one of the dominant crops and serves as a major source of staple food worldwide. In Pakistan, it contributes about 9.1% to the value added in agriculture and 1.7% to the gross domestic product (GDP) (ESP, 2017-2018). During 2016-2017, wheat was grown on an area of 8.73 million hectares, which produced 25.49 million tons of grains with average yield of 2919 kg ha⁻¹ in Pakistan (PBS, 2017-2018). Nevertheless, our national yields are still far below by comparing with other countries like USA, China and even with our immediate neighbor – India (Ahmed, 2015). Late planting, weeds infestation, drought stress, imbalance use of fertilizers and disease epidemics etc., are among the major reasons of low average yield (Hussain *et al.*, 2012a, 2016a, b; Shahzad *et al.*, 2016; Afridi *et al.*, 2017b).

Food security risks increased due to current circumstances of climatic revolution and its impact on some susceptible crops like wheat. However, during this year, shortfall in wheat production is attributed to decline in area sown, less and uneven rainfall, delayed and lengthy sugarcane crushing season, delayed harvesting of rice fine

cultivars, acute water shortages and heat stress (ESP, 2017-2018; PBS, 2017-2018). During past half decade, the incidence of rainfall amplified during peak growth stage of wheat which made climate conducive for occurrence of different diseases *i.e.*, stripe rust, fusarium head blight, powdery mildew, black point (kernel smudge) and karnal bunt (*Tilletia indica*). Stripe rust (*Puccinia striiformis* f. spp. *tritici*) mainly expands in moist and cool weather conditions (Afridi *et al.*, 2017b). The urediniospores of the said fungus are lengthened and lay down in linear rows between leaf veins and it produces black teliospores in late season (Chen *et al.*, 2014).

During 2017, most important disease of wheat was stripe rust, following a trend of recent years (Hollandbeck *et al.*, 2017; Waqar *et al.*, 2018). Percent yield loss during 2017 was 8.6%, which was lower than 2016 (9.1%) and 2015 (15.4%) but still well above the last 05, 10 and 20-year averages (6.63, 4.92 and 3.77%, respectively). The continued slight decrease in yield loss due to stripe rust might be due to continued foliar spray of fungicide used by growers in response to the very high yield losses occurred during 2015. This may have managed to keep the fungus at bay and minimize losses for a second year in a row.

In Pakistan, during mid 1990s severe epidemics have been caused by *Puccinia striiformis* causing economic losses in wheat cultivars Pirsabak-85 and Pak-81 which were grown on a larger area in Khyber Pakhtunkhwa, Pakistan (Afridi *et al.*, 2017b). The rust resistance of these cultivars was overcome by a new race during 1994-1995 and caused rust epidemic in this province, with 40% losses in grain yield (Morgounov *et al.*, 2004; Afzal *et al.*, 2007). Wheat cultivars Pirsabak-85 and Pak-81 were replaced by cultivar Inqilab-91 and cultivated on 80% of the area, posing a high-risk crop loss due to new races of stripe rust (Afridi *et al.*, 2017a, b). Development of new rust races (stripe rust) and favorable environmental conditions played a key role in rust epidemics during 2004-2005 and caused yield losses up to 70% especially in Inqilab-91 sown areas (Ahmad *et al.*, 2006).

Wide range of variation in wheat lines response to stripe rust proposed the development of new wheat cultivars with durable rust resistance and high grain yield (Chen, 2013). To control stripe rust of wheat, the only option is to develop disease resistant cultivars through cost-effective, environment friendly, efficient and sustainable approach (Paillard *et al.*, 2012; Afridi *et al.*, 2017b). However, a resistant cultivar does not remain resistant for a longer period (De-Vallavieille-Pope *et al.*, 2012). Wheat cultivars with a uniform genetic background of rust resistance put severe selection pressure on the pathogen and therefore, new pathotypes of stripe rust develop which break the resistance of cultivars (Chen *et al.*, 2014). A resistant cultivar is at 'Boom' when it produced more yield and 'bust' when the resistance is broken down after few years of release and severely reduced grain yield (Farahani *et al.*, 2014).

For developing wheat genotypes with good yield potential, it is crucial to study the genetic architecture of distinct wheat populations, legacy configuration of yield attributing traits and correlation of yield with yield contributing traits under present environmental conditions. Bolder wheat grains with high 1000-grain weight have better quality traits and ensure healthier germination during sowing (Afridi *et al.*, 2017b).

Different biometrical approaches like diallel and line × tester analyses are designed by Hayman (1954a, b), Griffing (1956) and Kempthorne (1957) for genetic analysis of various traits in different crops. Based on diallel analysis, the nature of gene action has been reported in several studies (Cheruiyot *et al.*, 2014; Farahani *et al.*, 2014; Afridi, 2016; Afridi *et al.*, 2017a, b; Ahmed *et al.*, 2017, 2018; Würschum *et al.*, 2018), however, most of the times the results remained discordant. Hence, the present study was designed with the aim to study the inheritance of stripe rust resistance and yield traits in wheat.

Materials and Methods

Experimental Site and Crop Seasons

The said study was carried out during three consecutive growing seasons *i.e.*, 2014-2015, 2015-2016 and 2016-2017

at Cereal Crops Research Institute (CCRI), Pirsabak - Nowshera, Pakistan.

Breeding Material and Procedure

The breeding material comprised of six diverse bread wheat cultivars for earliness and yield traits *i.e.*, Pirsabak-85, Khyber-87, Saleem-2000, Pirsabak-04, Pirsabak-05 and Shahkar-13 (Table 1). These six wheat cultivars were crossed in a half-diallel fashion to develop 15 F₁ hybrids during 2014-2015. During 2015-2016, the F₁ hybrids were sown and selfed to advance the generation. During 2016-2017, parental cultivars and F₁ hybrids with two replications, and parental cultivars + F₂ populations with three replications were grown in a randomized complete block design (RCBD) in same field. The sub-plot size was 3 × 0.9 m².

Crop Husbandry

Before sowing the field was well irrigated to create conditions conducive for seedbed preparation. The field was ploughed with deep plough then harrowed with planking each time to make the soil loose, fine, leveled and pulverized. The fertilizer was applied at the rate of 120:90:60 kg ha⁻¹ of NPK, respectively. All P₂O₅, K₂O and half N were applied at sowing time and the remaining half N was applied in two split doses with first and second irrigations. Sowing was carried out during 2nd week of November. In F₁ generation, single seed per hill was planted while in F₂ populations and parental genotypes the seed rate was maintained as 120 kg ha⁻¹ (25.5 g per sub-plot). Overall, four irrigations have been given to the crop every year. The dominant weeds were *Avena fatua*, *Chenopodium album*, *Chenopodium murale*, *Convolvulus arvensis*, *Cynodon dactylon*, *Malva parviflora*, *Melilotus indica*, *Medicago denticulata*, *Phalaris minor* and *Rumex dentatus*. The broad and narrow-leaved weeds were controlled with Buctril Super (750 mL ha⁻¹) and Puma Super (1250 mL ha⁻¹), respectively, however, the left over weed plants were removed manually. The randomly selected plants were harvested on single plant basis and used for data recording separately after threshing.

Data Collection

Scoring of stripe rust: To create inoculum pressure of *Puccinia striiformis* f. sp. *tritici* (PST), the wheat cultivar 'Morocco' which is highly susceptible to all races of rusts, was grown in two spreader rows around the experimental material. For artificial inoculation the spores of stripe rust were collected from cultivar Morocco and the suspension of urediospores was made in sterile distilled water with 2-3 drops of tween-20. In the evening time and at the booting stage of crop, the suspension of 0.1 g spore in 1-1 water was sprayed with hand sprayer to uniformly inoculate the parental genotypes, and F₁ and F₂ populations.

Table 1: Parental genotypes with local names, parentage, origin, Yr genes and yield traits

Parental cultivars	Pedigree	Resistance to Yr*	Yr genes**	Plant Color‡	Grains spike ⁻¹ §	Potential yield (kg ha ⁻¹) €
Pirsabak-85	KVZ/BUSHS/KAL/BB (CIMMYT)	Susceptible	Yr7,Yr9	Green	73	6000
Pirsabak-04	KAUZ/STAR (CIMMYT)	Moderately Susceptible	Yr18	Waxy green	75	6000
Pirsabak-05	MUNIA/SHTO//AMSEL (CIMMYT)	Resistant	-	Dark green	63	5500
Shahkar-13	CMH84.339/CMH78.578//MILAN (CIMMYT)	Resistant	Yr17	Waxy green	69	5500
Saleem-2000	CHAM-6//KITE/PGO (CIMMYT)	Moderately Susceptible	Yr18	Waxy green	64	6000
Khyber-87	KVZ/TRM//PTM/ANA-CM 43930 (CIMMYT)	Susceptible	Yr9+	Green	71	4500

CIMMYT: International Maize and Wheat Improvement Center

* Cultivars Pirsabak-05 and Shahkar-13 are rusts resistant cultivars while Pirsabak-85, Khyber-87, Saleem-2000 and Pirsabak-04 are rust susceptible genotypes. Crop Disease Research Institute NARC, 2014-15, 2015-16

** Qamar, M., S.D. Ahmad and M. Asif. 2012. Determination of levels of resistance in Pakistani bread wheat cultivars against stripe rust (*Puccinia striiformis*) under field conditions. *Afr. J. Agric. Res.*, 7: 5887-5897

‡ Afridi, K., 2016. Inheritance of yellow rust resistance and glutenin content in wheat. Ph.D Dissertation, Department of Plant Breeding and Genetics, The University of Agriculture, Peshawar – Pakistan

§ Phenotypic observations

€ Respective varietal proposal

The data on stripe rust was documented on flag leaves at the peak stage of epidemic development of rust on the leaves following modified Cobb's scale (Ali *et al.*, 2014) while host response was recorded according to Cheruiyot *et al.* (2014) (Table 2).

Yield Traits

The area of flag leaf, 1000-grain weight and grain yield was recorded using randomly selected 10 plants in F₁ hybrids and 20 plants in F₂ populations and parental genotypes. Area on flag leaf was determined at post-anthesis stage (Francis *et al.*, 1969). All the individual plants were threshed with single plant thresher. A descriptive sample of 1000 grains was used in each entry/replication and weighed with an electric balance to record the 1000-grain weight. By weighing the grains of 10 plants in F₁ hybrids and 20 plants in F₂ populations and parental cultivars in each genotype/replication, and then averaged for getting grain yield per plant.

Biometrical Analyses

Collected data were subjected to analysis of variance (ANOVA) according to Steel *et al.* (1997). After getting significant mean differences, the diallel analysis was further carried out (Hayman, 1954a, b; Mather and Jinks, 1982; Singh and Chaudhary, 1985). In F₂ populations, the formulae were modified to calculate the components of genetic variance as proposed by Verhalen and Murray (1969).

Results

Mean differences among parental genotypes and their F₁ and F₂ populations for stripe rust resistance, area of flag leaf, 1000-grain weight, and grain yield were significant ($p \leq 0.01$) (Table 3). Adequacy of the additive-dominance model was tested through three scaling tests (t^2 test, regression, and arrays analysis), and the model was found partially adequate for all the traits in both generations (Table 4). Results pertaining to genetic analysis for studied traits are provided as follows.

Table 2: Scale for scoring of data on stripe rust

Host response	Abbreviated sign	Host reaction
Immune	I	0.0
Traces	T	0.1
Resistant	R	0.2
Resistant to moderately resistant	RMR	0.3
Moderately resistant	MR	0.4
Moderately resistant to moderately susceptible	M	0.6
Moderately susceptible	MS	0.8
Moderately susceptible to susceptible	MSS	0.9
Susceptible	S	1.0

Coefficient of infection (C.I.) = Severity × Value of host reaction, Severity (%): 0-100 (Cheruiyot *et al.*, 2014)

Table 3: Mean square for various traits in 6 × 6 F₁ and F₂ half diallel crosses of wheat

Variables	F ₁ /F ₂	Mean squares				CV%
		Genotypes	Parents	F ₁ /F ₂	Parents vs. Error F ₁ & F ₂	
d.f.	F ₁	20	5	14	1	20
	F ₂	20	5	14	1	40
Stripe rust resistance	F ₁	45.09**	140.33**	2.26**	168.52**	0.0804 15.13
	F ₂	155.77**	379.11**	58.01**	405.10**	2.92 16.96
Area of flag leaf	F ₁	21.74*	22.67*	19.97*	41.77*	7.86 7.9
	F ₂	27.97**	33.59**	14.47**	188.97**	1.46 3.61
1000-grain weight	F ₁	5.01**	7.88**	4.32**	0.40	1.07 2.61
	F ₂	98.34**	193.95**	61.24**	139.83**	8.03 7.69
Grain yield	F ₁	40.29**	51.95**	27.53**	160.7**	8.32 9.2
plant ⁻¹	F ₂	76.98**	140.50**	46.78**	182.11**	13.62 15.31

*, ** = Significant at $P \leq 0.05$ and $P \leq 0.01$, NS = Non-significant

Stripe Rust Resistance

For stripe rust resistance, significant ($p \leq 0.01$) values of genetic components *i.e.*, 'a' and 'b' suggested the key role of additive and non-additive genes in both generations (Table 5). Significant ($p \leq 0.01$) values of 'b₁' specified the occurrence of directional genes in the F₁ and F₂ generations. Significant ($p \leq 0.01$) values of 'b₂' indicated asymmetrical gene distribution among the parental cultivars in both generations. Specific gene effects were found in F₂ due to significant ($p \leq 0.01$) value of 'b₃' whereas in F₁ generation no specific gene effects were observed due its non-significant value.

Table 4: Scaling test for various traits in 6 × 6 F₁ and F₂ half diallel crosses of wheat

Variables	F ₁ /F ₂	t ² test	Regression analysis		Arrays analysis		Conclusion
			b ₀	b ₁	Wr + Vr	Wr - Vr	
Stripe rust resistance	F ₁	-0.1120 ^{NS}	-0.0087 ^{NS}	0.0792 ^{NS}	1.1557 ^{NS}	0.2658 ^{NS}	Partially adequate
	F ₂	-0.0014 ^{NS}	0.0252 ^{NS}	-0.0307 ^{NS}	1.9676 ^{NS}	0.6232 ^{NS}	Partially adequate
Area of flag leaf	F ₁	-0.0095 ^{NS}	0.4164 ^{NS}	-0.6661 ^{NS}	0.8915 ^{NS}	1.9192 ^{NS}	Partially adequate
	F ₂	-0.0146 ^{NS}	0.3427 ^{NS}	-0.5172 ^{NS}	1.3770 ^{NS}	0.2025 ^{NS}	Partially adequate
1000-grain weight	F ₁	-0.0022 ^{NS}	0.3901 ^{NS}	-0.4383 ^{NS}	2.0584 ^{NS}	2.1415 ^{NS}	Partially adequate
	F ₂	-0.1115 ^{NS}	0.1012 ^{NS}	-0.1546 ^{NS}	1.2716 ^{NS}	0.2134 ^{NS}	Partially adequate
Grain yield plant ⁻¹	F ₁	-0.0159 ^{NS}	0.1626 ^{NS}	-0.2420 ^{NS}	1.1571 ^{NS}	0.7899 ^{NS}	Partially adequate
	F ₂	-0.0283 ^{NS}	0.2220 ^{NS}	-0.3788 ^{NS}	1.1864 ^{NS}	1.1848 ^{NS}	Partially adequate

NS = Non-significant

Table 5: Genetic analysis for various traits in 6 × 6 F₁ and F₂ half diallel crosses of wheat

Source of variation	d.f.		Stripe rust resistance		Area of flag leaf		1000-grain weight		Grain yield plant ⁻¹	
	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂
Replications	1	2	1.14	4.56	4.66	8.73 ^{**}	18.67 ^{**}	28.24 [*]	13.71	26.79
A	5	5	91.04 ^{**}	424.04 ^{**}	61.34 ^{**}	58.99 ^{**}	17.73 ^{**}	263.79 ^{**}	66.37 ^{**}	182.28 ^{**}
B	15	15	37.4 ^{**}	65.12 ^{**}	8.25	17.58 ^{**}	0.78	38.96 ^{**}	31.83 ^{**}	41.97 ^{**}
b ₁	1	1	210.04 ^{**}	401.94 ^{**}	39.01 [*]	188.93 ^{**}	0.40	126.05 ^{**}	159.72 ^{**}	182.32 ^{**}
b ₂	5	5	68.38 ^{**}	83.12 ^{**}	4.74	5.09 [*]	0.29	11.29	11.27	19.6
b ₃	9	9	1.01	17.7 ^{**}	6.78	5.48 ^{**}	1.09	44.65 ^{**}	29.05 ^{**}	38.81 [*]
Error	20	40	1.98	47.07	7.97	1.46	1.07	8.15	8.31	13.62

*, ** = Significant at P ≤ 0.05 and P ≤ 0.01, NS = Non-significant

Table 6: Genetic components of variance for various traits in 6 × 6 F₁ and F₂ half diallel crosses of wheat

Genetic Components	Stripe rust resistance		Area of flag leaf		1000-grain weight		Grain yield plant ⁻¹	
	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂
D	69.94 [*] ± 1.90	125.43 [*] ± 9.72	7.05 ± 6.60	10.69 [*] ± 2.10	3.46 [*] ± 1.30	59.12 [*] ± 11.67	21.49 [*] ± 10.16	42.41 [*] ± 12.97
H ₁	64.80 [*] ± 1.99	81.72 [*] ± 8.3	4.85 ± 8.09	15.89 [*] ± 2.37	0.32 ± 0.87	41.89 [*] ± 9.51	45.33 [*] ± 13.77	40.33 [*] ± 12.78
H ₂	39.79 [*] ± 1.19	57.78 [*] ± 5.53	5.6 ± 6.32	14.73 [*] ± 2.07	0.54 ± 0.71	40.45 [*] ± 8.23	43.56 [*] ± 11.83	37.71 [*] ± 10.70
F	82.58 [*] ± 2.54	91.48 [*] ± 11.29	-9.47 ± 6.18	2.27 ± 2.12	-1.19 ± 1.10	22.72 ± 12.09	10.28 ± 11.68	20.40 ± 14.44
h ²	54.56 [*] ± 2.82	86.55 [*] ± 13.47	10.63 ± 11.41	40.57 [*] ± 6.77	-0.11 ± 0.55	25.89 [*] ± 13.00	49.48 [*] ± 22.54	37.14 ± 19.43
E	0.06 ± 0.01	0.95 [*] ± 0.16	3.95 ± 0.95	0.49 [*] ± 0.08	0.0005 ± 0.12	2.65 [*] ± 0.44	4.49 [*] ± 1.04	4.42 [*] ± 0.70
F ₁ : √H ₁ /D, F ₂ : √1/4H ₁ /D	0.96	0.81	0.83	1.22	0.31	0.84	1.452	0.98
H ₂ /4H ₁	0.15	0.18	0.29	0.23	0.42	0.24	0.24	0.23
KD / KR	4.17	1.58	0.11	1.09	0.28	1.26	1.39	1.28
h ² /H ₂	1.65	1.79	2.28	3.30	-0.25	0.77	1.36	1.18
Heritability (bs)	0.99	0.97	0.70	0.95	0.83	0.92	0.80	0.83
Heritability (ns)	0.38	0.65	0.60	0.54	0.78	0.60	0.30	0.47

* In F₁ parameter value is significant when it exceeds 1.96 after dividing it by its standard error. In F₂ parameter value is tested by 't' test at n-2 d.f. after dividing it by its standard error

Genetic components (D, H₁, H₂, F, h²) and E were significant in both generations which evidenced that both additive and dominance have played a key role in the inheritance of yellow rust resistance (Table 6). However, values of H₁ and H₂ were less than D in F₁ and F₂ generations, which demonstrated the vital role of additive gene action. Average degrees of dominance were less than unity (0.96, 0.81) which also suggested additive gene action in F₁ and F₂ populations. Unequal H₁ and H₂ components exhibited an asymmetrical distribution of positive and negative genes among the parental genotypes for stripe rust resistance in both generations, and it was confirmed by the ratios of H₂/4H₁ (0.15, 0.18). Positive F-value indicated the important role of dominant genes in both generations and the same was also authenticated by the ratios of dominant and recessive genes (4.17, 1.58) in the parental cultivars for stripe rust resistance in both generations. The values of h² were positive in both generations and revealed that dominant genes were acting

mostly towards the susceptibility. Significant positive values of the environmental component in both generations illustrated the primary role of environment in the inheritance of said trait. Broad-sense heritability values (0.99, 0.98) were greater than narrow sense (0.38, 0.65) in F₁ and F₂ generations, respectively (Table 6). High broad-sense heritability estimates demonstrating less effect of environment on the expression of stripe rust resistance. However, narrow-sense heritability for stripe rust resistance was moderately high indicating that additive effects of genes were essential in the inheritance of said trait in F₂ generation.

The Vr-Wr graphs revealed that regression line intercepted the covariance line above the origin, which revealed partial dominance type of gene action in both generations (Fig. 1a, b). The scattered positions of cultivars on regression line illustrated that cultivars Pirsabak-04, Pirsabak-05, Shahkar-13 and Saleem-2000 had maximum dominant genes, whereas Pirsabak-85 had

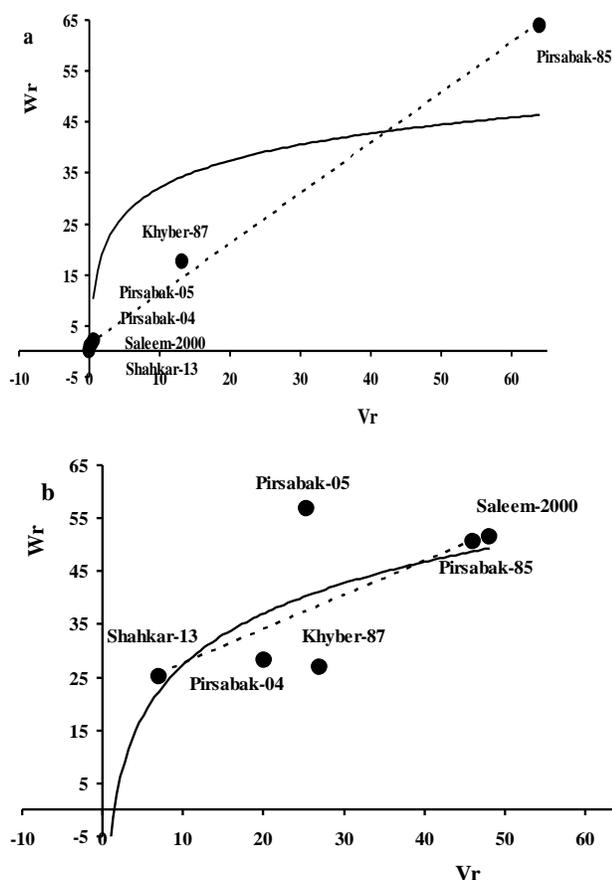


Fig. 1: Vr-Wr graph for stripe rust resistance in 6 × 6 (a) F₁ and (b) F₂ half diallel crosses of wheat

maximum recessive genes in F₁ generation. In the F₂ generation, parental genotype Shahkar-13 had maximum dominant while cultivar Saleem-2000 had maximum recessive genes to govern the inheritance of stripe rust resistance.

Area of Flag Leaf

The component 'a' was significant ($p \leq 0.01$) while 'b' was non-significant in F₁ generation whereas both components (a, b) were significant ($p \leq 0.01$) for area of flag leaf in F₂ populations (Table 5). Hence, both additive and non-additive genetic components were important in the inheritance of area of flag leaf in segregating generation. Significant 'b₁' component specified directional dominance in F₁ ($p \leq 0.05$) and F₂ ($p \leq 0.01$) populations. However, non-significant 'b₂' component showed symmetrical gene distribution among parents in F₁ generation. Asymmetrical gene distribution was observed in F₂ generation due to significant 'b₂' ($p \leq 0.05$) component. Significant ($p \leq 0.01$) value of 'b₃' demonstrated the residual dominance effects for area of flag leaf in the F₂ generation, which indicated the involvement of dominance deviation.

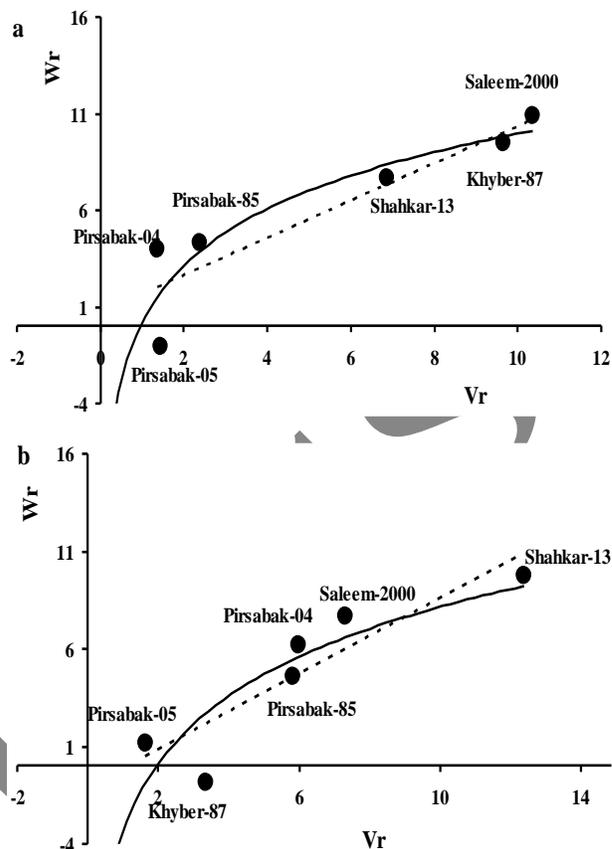


Fig. 2: Vr-Wr graph for area of flag leaf in 6 × 6 (a) F₁ and (b) F₂ half diallel crosses of wheat

All the components of genetic variation (D, H₁, H₂ and F) were non-significant whereas E was significant for area of flag leaf in the F₁ generation (Table 6). The average degree of dominance was less than unity (0.83), which confirmed that area of flag leaf was controlled by the additive type of gene action in the F₁ generation. The F value was negative for area of flag leaf, which suggested that greater number of recessive alleles were owned by the parental genotypes in the F₁ generation, and it was also authenticated by the ratio of dominant and recessive genes in the parental lines (0.105). In the F₂ populations, the components of genetic variance displayed that D, H₁, H₂, h² and E were significant for area of flag leaf (Table 5). Equally additive and non-additive components of genetic variance were crucial for legacy of the trait under study. However, the value of H₁ was greater than D component in F₂ population which revealed that area of flag leaf was controlled by non-additive gene action in the F₂ generation. The average degree of dominance for area of flag leaf was greater than unity, which suggested that the character was regulated by over-dominance type of gene action in the F₂ generation. The value of F was non-significant but positive for area of flag leaf, which proposed that greater number of dominant alleles were carried by the parental genotypes in the F₂ generation,

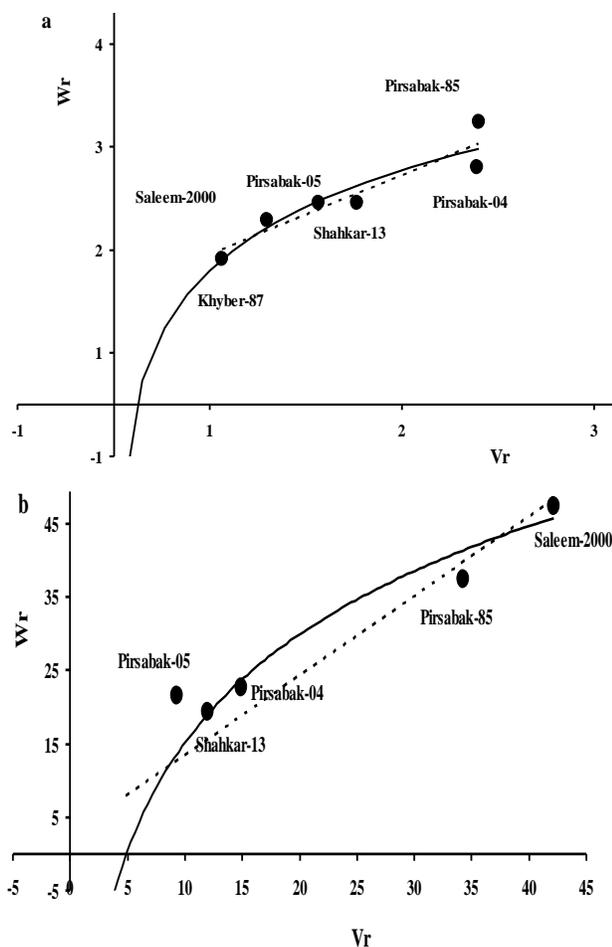


Fig. 3: Vr-Wr graph for 1000-grain weight in 6×6 (a) F_1 and (b) F_2 half diallel crosses of wheat

and it was also supported by the ratio of dominant and recessive genes in the parental cultivars (1.09). Unequal H_1 and H_2 components and the ratios of $H_2/4H_1$ (0.29, 0.23) exhibited an asymmetrical distribution of positive and negative genes among the parental cultivars for area of flag leaf in both generations. Results further revealed that additive and non-additive gene actions played a key role in genetic regulation of this character. Broad-sense heritability values (0.70, 0.95) were comparatively high than narrow-sense heritability (0.60, 0.53) in F_1 and F_2 generations, respectively (Table 6). Greater broad sense heritability than narrow-sense, showed the primary role of genetic variance as compared to environmental variance.

According to Vr-Wr graph, the regression line cut off the Wr-axis above the point of origin and partial dominance gene action was responsible for controlling area of flag leaf in the F_1 generation (Fig. 2a). However, in the F_2 generation the inheritance of area of flag leaf was controlled by the over-dominance type of gene action as regression line touched the y-axis below the point of origin (Fig. 2b). The relative distribution of cultivars along the regression line revealed that

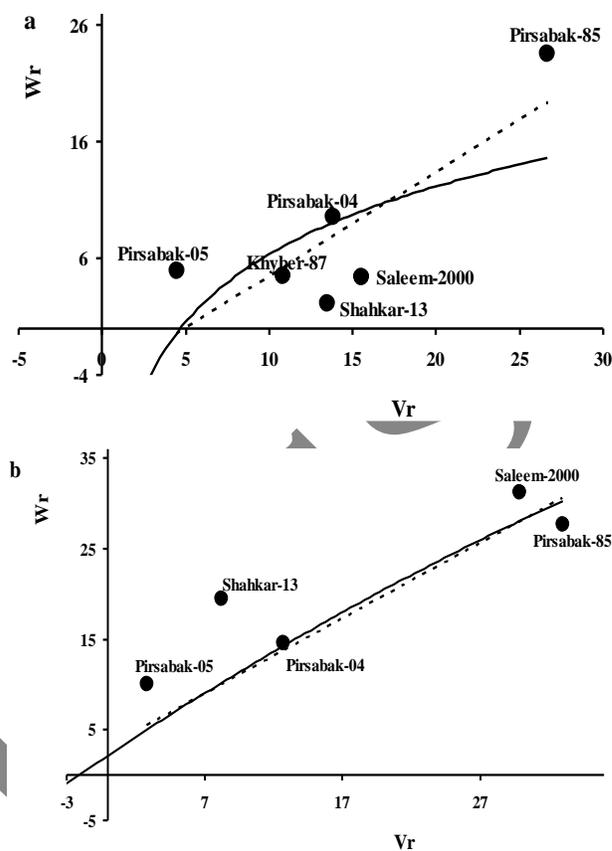


Fig. 4: Vr-Wr graph for grain yield per plant in 6×6 (a) F_1 and (b) F_2 half diallel crosses of wheat

Pirsabak-05 had maximum dominant genes and resides closer to the origin in both generations. Cultivars Saleem-2000 and Shakkar-13 had a maximum number of recessive genes as both of these cultivars were farthest from the origin.

Yield Traits

Significant ($p \leq 0.01$) mean squares were observed for component 'a' in both generations however, the value of component 'b' was non-significant and significant ($p \leq 0.01$) in the F_1 and F_2 generations, respectively for 1000-grain weight (Table 5). Hence, additive and dominant components of genetic variance were imperative for inheritance of the studied trait. Additive component was significant whereas all other components were non-significant for 1000-grain weight in the F_1 generation (Table 6). In F_2 generation, all the genetic components were significant except 'F' which was non-significant. Additive component was larger than dominance components in both generations which revealed that 1000-grain weight was managed by additive gene action. Average degrees of dominance were less than unity (0.31, 0.84) for 1000-grain weight in both generations. Unequal H_1 and H_2 components and the ratios of $H_2/4H_1$ (0.42, 0.24)

exhibited the asymmetrical distribution of positive and negative genes among the parental genotypes for 1000-grain weight in F₁ and F₂ populations, respectively. In F₁ and F₂ generations, h² and F values were negative and positive, showing more recessive and dominant genes, respectively. High broad (0.83, 0.92) and narrow-sense (0.78, 0.60) heritability values were recorded for 1000-grain weight in F₁ and F₂ generations, respectively (Table 6). Inheritance pattern for 1000-grain weight seemed to be of partial dominance, as the regression line cut off the Wr-axis above the point of origin in both generations (Fig. 3a, b). Cultivar Khyber-87 was near the point of origin and possessed maximum dominant genes in both generations. Parental cultivars *i.e.*, Pirsabak-85 and Pirsabak-05 reside far away from the point of origin and possessed maximum recessive genes in F₁ and F₂ generations, respectively.

Significant ($p \leq 0.01$) components *i.e.*, 'a' and 'b' were recorded for grain yield per plant which showed the involvement of additive and non-additive gene action in both generations (Table 5). Majority of the components of genetic variation were significant for grain yield in F₁ and F₂ populations (Table 6). The values of dominance components were greater than additive in the F₁ generation which revealed non-additive gene action in genetic control of grain yield per plant. However, the F₂ generation specified the greater role of the additive gene action. The values for average degree of dominance was greater (1.45) in F₁ and lesser (0.98) in F₂ than unity indicated the over-dominance type and additive type gene action, respectively. The value of h² was significant in F₁ and non-significant in F₂ populations, supporting the dominant gene action in F₁ and additive gene action in F₂ generation. Broad-sense heritability values (0.80, 0.83) were greater than narrow-sense (0.30, 0.47) for grain yield in F₁ and F₂ populations (Table 6). In Vr-Wr graphical analysis, the regression line cut off the Wr-axis below the point of origin which revealed the over-dominance type of gene action for grain yield per plant in the F₁ generation (Fig. 4a). In the F₂ generation, the regression line intercepted Wr-axis above the origin, suggesting the additive type of gene action for grain yield per plant (Fig. 4b). Cultivars Pirsabak-05 and Pirsabak-85 had the most dominant and recessive genes, respectively in both generations.

Results of the study revealed that additive type of gene action played a major role in controlling stripe rust resistance, area of flag leaf, 1000-grain weight and grain yield in both generations except grain yield in F₁ and area of flag leaf in F₂ populations. Therefore, these traits could be improved through selection in early segregating generations.

Discussion

Parental genotypes and their F₁ and F₂ populations possessed greater genetic variability by having significant differences for all the traits. Additive-dominance model was partially adequate for all the traits including stripe rust resistance in both generations. Past studies revealed partial adequacy for

area of flag leaf, 1000-grain weight and grain yield (Ahmad *et al.*, 2016) and grains per spike (Nazir *et al.*, 2014) in wheat. However, the additive-dominance model was fully adequate for area of flag leaf and yield traits (Nazir *et al.*, 2014), stem rust and yield traits (Cheruiyot *et al.*, 2014) in different wheat populations.

For stripe rust resistance, significance of genetic components suggested the key role of the additive and non-additive genes in both generations. However, additive component and average degrees of dominance suggested additive type of gene action in both generations. Therefore, desirable genotypes could be improved through simple selection in segregating populations. Similarly, Cheruiyot *et al.* (2014) mentioned the greater value of the additive genetic component for stripe rust resistance in advanced lines of wheat. Generation mean analysis showed that dominant effects were more important than additive for resistance to stripe rust (Farahani *et al.*, 2014). Specified preponderance of additive and dominant genes governed the partial resistance to stripe rust in parental cultivars and F₁ populations in wheat (Afridi *et al.*, 2017b). However, complete dominance was reported for stripe rust resistance in wheat genotypes (Farahani *et al.*, 2014). However, Afridi *et al.* (2017b) reported preponderance of nonadditive gene effects for resistance to stripe rust in F₁ and F₂ populations of wheat. Such contradictory findings might be due varied genotypic and environmental differences.

Present results revealed that majority of the genetic components were non-significant for area of flag leaf in F₁ generation. Similarly, non-significant components of genetic variance for area of flag leaf in wheat also supported the present results (Ahmad *et al.*, 2013). However, in present studies the additive genetic effects were more prominent than dominance. Involvement of the additive gene action in the expression of area of flag leaf was also reported in wheat under different environmental conditions (Afridi *et al.*, 2017b). In F₂ generation, the inheritance of area of flag leaf was controlled by over-dominance type of gene action. Selections in such promising hybrids could be utilized in hybrid wheat production to increase the wheat yield. Over-dominance type of gene action was reported for area of flag leaf in different wheat populations (Nazeer *et al.*, 2010; Nazir *et al.*, 2014; Ahmad *et al.*, 2016).

Additive component of variation was significant whereas other genetic components were non-significant for 1000-grain weight in F₁ populations. In F₂ populations, all the genetic components were significant; however, the magnitude of additive component was greater than non-additive which suggested early generation selection for 1000-grain weight. Significant of additive and dominance components for 1000-grain weight in F₂ populations proposed that selection could be practiced in early generations (Afridi *et al.*, 2017b). Past studies revealed that 1000-grain weight and other yield traits were controlled by additive type of gene action with partial dominance in different wheat populations (Nazir *et al.*, 2014).

However, over-dominance type of gene action was specified for 1000-grain weight in spring wheat (Nazeer et al., 2010; Hussain et al., 2012b). Significant and importance of both additive and dominance genetic effects for 1000-grain weight were reported in F₁ populations of wheat (Minhas et al., 2014). Contrasting views might be due to broad genetic make-up of the wheat genotypes and the genotype by environment interactions.

Components of the genetic variation were significant for grain yield in F₁ and F₂ populations. However, in F₁ generation the inheritance of grain yield was controlled by non-additive gene action while in F₂ generation the additive genetic component was responsible for inheritance of the said trait. The contradiction in genetic components of both generations might be due to residual heterozygosity in parents (Hayman, 1954a, b). The grain yield per plant could be improved in desirable genotypes by using simple selection in F₂ populations. However, over-dominance in F₁ generation could be used for exploitation of heterosis by selection in promising wheat F₁ populations. Greater values of dominance components than additive revealed that grain yield was controlled by dominant genes in spring wheat (Zare-Kohan and Heidari, 2012). For grain yield, additive gene action was confirmed by components of genetic variation and graphical analysis in wheat (Nazir et al., 2014; Ahmad et al., 2016). However, dominance effects were also found for grain yield in genetic analysis in wheat (Nazeer et al., 2010). Contradictions in past and present findings about F₁ and F₂ generations might be due to different genetic make-up of the wheat genotypes and the environment. Genetic components revealed that additive genetic effects were indispensable for majority of the traits. Therefore, selection in early segregating generations would be successful.

Conclusion

Greater genetic variability revealed by parental genotypes and their F₁ and F₂ populations for stripe rust resistance and yield traits. Additive-dominance model was partially adequate for rust resistance and yield traits, which allowed further genetic analysis in both generations. Due to preponderance of additive type of gene action for yellow rust resistance, 1000-grain weight and grain yield in F₂ populations, the pedigree method could be used to improve these traits. However, due to prevalence of over-dominance type of gene action for area of flag leaf in F₂ generation, bulk method would be preferred to improve the trait.

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